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A REVIEW OF WILLIAM DILLER MATTHEW'S CONTRIBUTIONS TO MAMMALIAN PALÆONTOLOGY

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The late William Diller Matthew, Professor of Palæontology and Director of the Museum of Palæontology in the University of California, and for many years Curator of the Department of Vertebrate Palæontology in the American Museum of Natural History, left to the world a legacy in the form of some two hundred and forty-four scientific papers, which deal for the most part with mammalian palæontology. He also imparted to many of his students and junior colleagues an active interest in palæontological exploration and in the advancement of the great theme of mammalian evolution to which he had contributed so much. Various general biographical articles¹ on Doctor Matthew having already been published, it would now seem both timely and useful to attempt a special review of his chief contributions to mammalian palæontology.

HIS EARLIER CONTRIBUTIONS TO KNOWLEDGE OF RECENT AND FOSSIL MAMMALS

Soon after Doctor Matthew's coming to the American Museum of Natural History in 1895, he was sent by Professor Osborn to Philadelphia to catalogue, pack up and ship to New York the great collections of Professor E. D. Cope, which had been purchased by the Museum. In this way Matthew came to know and admire Professor Cope and began the detailed task of checking Cope's identifications and revising his classifications, which was to occupy him, along with many other matters, for the next thirty-odd years.

In this fortunate way also he began his acquaintance with the mammals of the Basal Eocene of New Mexico, revising the combined collections of Professor Cope and that which had recently been made by Dr. Wortman for the Museum. The year 1896-97 was thus devoted to "A

¹Gregory, William K. 1930. William Diller Matthew, 1871-1930. *Natural History*, XXX, No. 6, pp. 664-666.

Gregory, William K. 1930. William Diller Matthew, Paleontologist (1871-1930). *Science*, LXXII, No. 1878, pp. 642-645.

Schuchert, Charles. 1930. William Diller Matthew, February 19, 1871-September 24, 1930. *Am. Jour. Sci.*, XX, December, 1930, pp. 483-484.

Osborn, Henry Fairfield. 1931. William Diller Matthew, F. R. S. *Bull. Geol. Soc. Amer.* (In press.)

Revision of the Puerco Fauna,"¹ Matthew's first extensive paper on fossil mammals. In this he made certain definite contributions toward the solution of many of the major problems dealt with in his subsequent papers. In this paper he confirms Dr. Wortman's division into two well separated faunas, the Puerco and the Torrejon, which are shown to be as different as any two successive Eocene formations.

The most important and original parts of the paper are those that deal with the Creodonta, the Condylarthra and the Foot Structure of Basal Eocene Mammals. The creodonts were represented by five families, including the Oxyclænidae, a group of genera with a remarkably primitive type of dentition, many of which had been placed among the Primates but which were now again referred to the Creodonta. To every one of these families Matthew later made important contributions, but in this paper only the initial steps were taken, by a careful revision of the genera and species. In discussing the Condylarthra of Cope, the important observation was made that this group of "protoungulates," as they had been called, is "nearly related to the early Creodonta and its hypothetical ancestral type or types would be strictly Creodont."

In the sections of the skeleton of *Euprotogonia* and on the Foot Structure of Basal Eocene Mammals it was pointed out that a review of the structure of the carpus and tarsus of Basal Eocene Primates, Creodonta, Condylarthra, Amblypoda, Edentata, did not support Professor Cope's view that in the primitive carpus and tarsus the proximal and distal rows of bones were arranged in vertical series like "unstruck bricks." On the contrary, "the conclusion to which the study of these feet leads, apart from any theoretical considerations, seems to me to be as follows:

"The primitive condition of the carpus was alternating, with the centrale present. By *absorption* of the centrale a serial carpus, except for the lunar-unciform contact, was produced. By fusion of the centrale with the scaphoid the alternating type of carpus would be maintained. That this primitive alternating carpus was preceded by an entirely serial carpus of the type of *Meniscotherium* is quite possible but there is no evidence of it.

"In the tarsus we find no evidence to support the theory of primitive serialism. Only in *Euprotogonia*, the most progressive of the group, do we find an approximately serial tarsus and this is accompanied by a slender foot adapted for running, and by reduced side toes. The

¹1897. Bull. Amer. Mus. Nat. Hist., IX, Art. XXII, pp. 259-323. 20 figs.

drift of all the evidence is toward relegating the primitive serial carpus and tarsus back into the unknown Cretaceous."

It may be noted that this virtual abandonment of Cope's theory of the origin of the ungulate carpus and tarsus if accepted would greatly weaken Cope's classification of the ungulate orders and his conclusions as to their relationships with each other and with the unguiculates. In the subsequent decades, as more and better preserved skeletons of Basal Eocene and Eocene mammals came to light, the correctness of Matthew's conclusion came to be fully realized by other palæontologists.

In 1898 his bibliography contains no entry, partly for the sufficient reason that the author was busy upon three important papers that appeared in 1899. In "A Provisional Classification of the Fresh-water Tertiary of the West"¹ the faunal lists of the successive horizons had been submitted to Professors Osborn, Cope, Scott and Dr. Wortman for approval or amendment and were based chiefly on Matthew's first-hand studies of the American Museum collections. A partial essay was made at a critical revision of the species. Thus was laid down the first extensive and critical basis for the expanded and revised lists of later years. Critical notes were also made on the so-called Lake Basins and Matthew's analysis of the later Tertiary horizons of the western states was given.

DEMOLITION OF THE "LAKE THEORY"

His second paper of the year 1899, "Is the White River Tertiary an Aeolian Formation?"² was a brilliant attempt to disprove the classical theory that the great fossil-mammal-bearing horizons of the western states were ancient "lake basins." By cumulative geologic and palæontologic evidence, this theory was shown to be untenable, while at the same time the author tried to establish the conclusion that at least the great bulk of the formations had been laid down as wind-blown loess on broad flood-plains or by rivers and streams. Soon afterward Hatcher, Osborn and others accepted at least the negative side of Matthew's paper but laid more stress on the periodic flooding of the "basins" by rivers.

"ANCESTRY OF THE CANIDÆ"

The third paper of 1899, "The Ancestry of Certain Members of the Canidæ, the Viverridæ and Procyonidæ,"³ was published in collaboration with Dr. J. L. Wortman. The sections by Matthew deal with the affini-

¹1899. Bull. Amer. Mus. Nat. Hist., XII, Art. III, pp. 19-75.

²1899. Amer. Naturalist, XXXIII, No. 389, pp. 403-408.

³1899. Bull. Amer. Mus. Nat. Hist., XII, Art. VI, pp. 109-139, Pl. vi, 10 figs.

ties of the Oligocene ('Miocene') Canidæ of North America and describe *Phlaocyon* as an ancestor of the Raccoons. Here, then, was the first of a series of papers on the ancestry of the Tertiary Carnivora, especially the Canidæ and Procyonidæ.

OBSERVATIONS ON THE CREODONTS

In 1900 only one short article appeared, but in 1901 two important papers were issued. In "Additional Observations on the Creodonta," Dr. Matthew addressed himself with great success to the problem of clarifying the hitherto confused relationships and classification of the families of the Creodonta, a subject to which he returned at intervals in later papers. The puzzling characters of *Clænodon* of the Arctocyoni-dæ were carefully analyzed. It was shown (*op. cit.*, p. 18) that "the Arctocyons were progressing towards the Bear line in all the most distinctive characters of both teeth and feet. But the wide gap between Lower Eocene and Middle Miocene makes any connection between the two somewhat uncertain. In the Canid line, on the other hand, we have a number of apparently intermediate stages known [leading from the dogs to the bears]. But these intermediate stages can not have been actually in the line of ascent; and even if they are unaltered descendants of more ancient types we still have a gap of some importance unbridged. The connection, moreover, is based on teeth alone. Professor Osborn, in discussing the evolution of the Mammalia remarks: 'The teeth and feet, owing to the frequent parallels of adaptation, may wholly mislead us if taken alone; when considered together they give us a sure key; for no case of exact parallelism in both teeth and feet between two unrelated types has yet been found or is likely to be' (Osborn, 1893, p. 10). If *Clænodon* be totally unrelated to the Ursidæ, it is an exception to this statement, and as far as I recall, the only one. And yet the evidence is very strong for deriving the Ursidæ from primitive Dogs." In later years Dr. Gidley again brought up the claims of *Clænodon* to be considered as possibly related to or near the line of ancestry of the bears but was vigorously opposed by Dr. Matthew.

"FOSSIL MAMMALS OF THE TERTIARY OF NORTHEASTERN COLORADO"

In the memoir entitled "Fossil Mammals of the Tertiary of North-eastern Colorado,"¹ the theory of lacustrine origin of the White River and Loup Fork groups was attacked in greater detail than in the brief

¹1901, Mem. Amer. Mus. Nat. Hist., I, pp. 353-446, Pls. xxxvii-xxxix, 34 figs.

article in the *American Naturalist*, and the theory of "flood-plain playa and æolian deposition" was defended with a wealth of arguments drawn from field observations and from an analysis of the faunas preserved in these formations. In the "Analyses and Discussion of the Faunæ," it was shown that "two distinct facies were presented by the fauna of each horizon [of the White River Oligocene], the characteristic fauna of the clays being widely different from that of the sandstones." The conclusion is reached (p. 371) that "the analogy of the clay fauna is with that of the modern plains, of the sandstone fauna with that of the modern forests (with some aquatic forms). In the clays we have hares, squirrels (cf. *Tamias*), vesper-mice and Ischyromids (cf. *Cynomys*) as the characteristic rodents; in the sandstones we have beavers. . . ." The analysis was continued throughout the fauna considered by orders and families. The general conclusion (p. 372) was as follows: "The above evidence seems to make it reasonably certain that the clays and sandstones contain respectively a plains and forest fauna, the latter including some aquatic types. And the occurrence of two such faunæ in these circumstances exactly accords with the theory of terrestrial and flood-plain origin of these beds as set forth in the previous section of this paper, while it seems utterly inexplicable on the theory of their lacustrine origin."

From the section dealing with the systematic descriptions in this paper only two or three especially interesting items may be noted here. A carefully worked-out reconstruction of the skeleton of the primitive canid *Cynodictis gregarius* was given. This animal was so primitive that its skeleton as a whole was strikingly like that of a viverrine; with curved backbone, long tail, short spreading forefeet. In other words, it lacked the cursorial specializations of the later dogs.

Under the section dealing with the Felidæ, one finds a remarkably interesting discussion of the rise of the sabre-like canines of the Sabre-tooth. The idea that the tusks were used as stabbing weapons but used with the mouth closed was refuted by the fact that the special construction of the mandible permitted the jaw to drop even far below the level of the tips of the upper canines. Associated changes, especially in the size and position of the mastoid processes, indicate unusual strength in certain muscles involved in a stabbing movement of the head. The conclusion was reached that their prey consisted of "large short-necked animals, probably thick-skinned," and that "their most advantageous method of attack was to inflict stabbing and ripping cuts at points where an artery could be reached, using their short, broad and powerful forefeet as fulcrums, and probably bleeding the animal to death."

Passing to the Artiodactyla, the author gave an analysis of the Oreodonts (p. 395) from a combined evolutionary and taxonomic viewpoint. By examining his tables, etc., one may readily grasp not only the chief contrasts between the principal genera but the successive stages in the differentiation of the more specialized from the less specialized types. This was characteristic of Matthew that while scrupulously accurate as to facts he never lost the evolutionary and chronologic perspective and that he was never satisfied with merely recording differences but insisted on understanding their drift or meaning.

In the section on the Camelidæ the detailed description of new material is preceded by an analysis of the distinctive characters and of the genera and species of Loup Fork Camels. In the description of *Alticamelus*, the giraffe-camel, the following passage occurs: "The discovery of this specimen introduces to science one of the most interesting instances of convergence yet observed. The effect of extreme height, in order to enable the animal to feed upon the inaccessible foliage of high and thorny shrubs, is obtained in this species, as in the giraffe, by the elongation of the neck vertebræ and the legs. But the giraffe is derived from the early antelopes and *Alticamelus* from early camels and the difference of origin has caused the attainment of the desired result in a somewhat different manner." The subsequent analysis of the osteologic resemblances and differences between the giraffe-camel and the giraffe is full of meaning and value.

In the next year (1902) eight rather brief papers appear in his bibliography, each embodying some record of his activities either in preparing for exhibition the hall of vertebrates in the Museum or in describing material collected by himself and his colleagues during the field parties in Texas, Colorado and elsewhere. Of these, the article entitled "New Canidæ from the Miocene of Colorado"¹ is of special interest because it contains the first outline of his theory of the Holarctic origin and dispersal of the principal families of placental mammals, under the control of secular climatic changes.

Thus by the close of his first five years at the Museum we find that he had already begun to deal in a very constructive way with most of the great problems that continued to engage his energetic interest for the rest of his life. In reading any of his earlier papers one gets the impression that only in a few places could they be considered as superseded or out of date a quarter of a century later, even where much more complete

¹1902, Bull. Amer. Mus. Nat. Hist., XVI, Art. XXI, pp. 281-290.

material has since been discovered. This is perhaps because he combined high originality and initiative with a great reserve of conservatism and caution.

MEMOIR ON THE CARNIVORA AND INSECTIVORA OF THE BRIDGER BASIN

At this point it appears advisable, however, to abandon a chronologic review of his many important publications and to attempt brief summaries in a number of different fields.

In his subsequent contributions on the Creodonta, he described many new species, and by means of more and better material was able to settle many questions left open in previous papers. His classification of the group was given in the Memoir on "The Carnivora and Insectivora of the Bridger Basin, Middle Eocene" (1909),¹ and in "A Revision of the Lower Eocene Wasatch and Wind River Faunas" (1915).² Following Cope, Matthew defined the suborder Creodonta as distinguished from the Fissipedia by such primitive characters as the small simple brain, the separate scaphoid, lunar and centrale, the flat astragalar trochlea, the presence of five digits on the manus and pes (except in more advanced forms), the retention of an entepicondylar foramen on the humerus and of a third trochanter on the femur.

At first Matthew accepted the grouping by earlier authors into Adaptive and Inadaptive sections of the Creodonts, adding thereto a third section, Primitive Creodonts, to contain the Oxyclænidae, whose status as creodonts he had been able to confirm. Later he invented the highly useful terms, Procreodi, Acreodi, Pseudocreodi and Eucreodi, which were given in reference to the contrasting characters of the shearing teeth in the different families. In the primitive Oxyclænidae the shearing function was not yet concentrated on any of the cheek teeth, and they were therefore named Procreodi. To this division the Arctocyoniidae were transferred in 1915, as a result of the discovery of the Lower Eocene genus *Thryptacodon* of Matthew, which clearly tended to connect the Arctocyoniidae with the more primitive family of Oxyclænidae. In the Eucreodi, including only the Eocene family of the Miacidae, the specialized carnassial function was confined to the fourth upper premolar and the first lower molar exactly as in the modern Fissipedia. In the Pseudocreodi, very similar appearing carnassial teeth were developed not on

¹1909. Mem. Amer. Mus. Nat. Hist., IX, Pt. VI, pp. 291-567, Pls. XLII-LI, 118 figs.

²1915. (With Walter Granger.) Part I (By W. D. Matthew): Order Ferae (Carnivora), Suborder Creodonta. Bull. Amer. Mus. Nat. Hist., XXXIV, Art. I, pp. 1-103. Part II (By W. D. Matthew): Order Condylarthra, Family Hyopsodontidae. *Idem*, XXXIV, Art. IX, pp. 311-328. Part IV (By W. D. Matthew): Entelonychia, Primates, Insectivora (part). *Idem*, XXXIV, Art. XIV, pp. 429-483.

p^4 and m_1 but on one or another of the true molars (on m^1 and m_2 in the Oxyænidæ and on m^2 and m_3 in the Hyænodontidæ). In the Acreodi, including the Mesonychidæ and the related family of Triisodontidæ, there were no carnassials. The characters of the ungual phalanges, whether unfissured or fissured or flattened, were also used in this primary division.

Matthew retained the Eucoreodi in the suborder Creodonta, partly because Cope, in his definition of the suborder, had included representatives of both the divisions afterward called Inadaptive and Adaptive Creodonts and because he (Matthew) was indisposed to follow to extremes either the group or the linear theory of classification and regarded a combination of the two as more practical and convenient and as best expressing the relationships of groups from both the morphological and phyletic standpoints. "As regards the Eocene Carnivora," he continues (1909, p. 320), "it appears better to retain the generally accepted arrangement as more natural and convenient. They form a natural and readily definable suborder, divisible into three groups of about equal value, besides a few primitive forms of uncertain affinities. One of these groups gave rise to the Fissipedia by assumption of a number of progressive characters; the others became extinct without assuming these progressive characters. The conversion of the adaptive Creodonts into Fissipedia and the disappearance of the inadaptive groups nearly coincide with the end of the Eocene. If on the other hand we place the Adaptive Creodonts in the Fissipedia, we not only remove them from their nearest relatives and make it difficult to adequately define the inadaptive groups so as to exclude them, but we obscure, as it seems to me, the real relationships of the Eocene Carnivora to each other and to adjoining orders, as well as to the more modernized group. The attempt to distribute the adaptive genera into the modern families is open to more serious objections, as even with a complete knowledge of the skeleton it is not always possible to be sure of their exact relationship to the living carnivora, and to associate the closely allied Eocene genera with the widely separated modern families to which they may be ancestral, not only obscures their real relations, but makes their position dependent upon very transitory and uncertain theories of phylogeny."

As regards the origin of the Fissipedia, Matthew suggested in the same memoir (1909, p. 351) that "it appears probable that in the Miacinæ and Viverravinæ we have the beginning of the differentiation into Arctoid and Aeluroid carnivora. . . ."

The phylogeny of the bears continued to offer difficulties at this

time (p. 351) but as the years passed and he saw more and more of both dogs and bears as well as of alleged intermediate genera, he became firmly convinced that the bears had been derived from dogs of some sort.

In this memoir (1909), Matthew dealt rather fully and incisively (pp. 335-339) with Dr. Wortman's idea that the Fissipedia, Creodonta and Insectivora are independently derived from the Upper Cretaceous marsupials as exemplified by the Laramie genus *Didelphops*, citing very strong adverse evidence against this view and defending the contrary thesis that the Creodonta and all other placentals are separated from the carnivorous marsupials "by numerous and important distinctions which bespeak a very remote relationship between the Marsupials and the Eutherian groups."

One of the most important sections of the Memoir on the Bridger Carnivora and Insectivora was that which dealt with the stratigraphy and faunal divisions of the Bridger formation. This extensive palæontological and geological survey had been made for the U. S. Geological Survey by Matthew and Granger during the seasons of 1902 and 1904, in determining faunal levels in the Bridger formation, under instructions from Professor Osborn and in connection with the latter's investigations on the phylogeny of the titanotheres. They were able to establish the existence of five successive major faunal levels containing numerous subdivisions and recognizable at many different localities in the Bridger basin.

On the basis of the faunal lists recording the precise level of each species, Matthew distinguished the Lower from the Upper Bridger and was able in the case of a number of species to trace the changes in the premolar and molar teeth as one passed from the lower to higher levels. This was especially well shown in the study of nearly three hundred specimens of the genus *Hyopsodus* from successive levels in the Bridger basin. This genus was provisionally referred to the order Insectivora, the latter being taken in a very broad sense. The opinion was expressed, however (p. 512), that "its affinities are in reality closer to the Condylarthra than to the more typical Insectivora," and later the discovery of better skeletal material confirmed this view, so that the family Hyopsodontidæ was transferred to the Condylarthra as a very primitive division of that order. Another puzzling form, provisionally classed as an insectivore, was the genus *Pantolestes*, which was shown to possess indications of aquatic habits in several parts of the skeleton.

In short, this memoir abounds in important and far-reaching facts,

analyses and conclusions. We may cite, for instance, the provisional phylogenies of the Miacidæ (p. 353) and Hyænodontidæ (p. 467), the author's comparative drawings illustrating the dentitions of carnivores of the different families, his studies on the basicranial region and dental foramina of carnivores and insectivores, his demonstration (p. 430) of the progressive lengthening of the metatarsal and first phalanx as compared with the length of the femur in aquatic as contrasted with terrestrial carnivores, his remarks (p. 549) on the value of the astragalus in Ordinal Classification. It is greatly to be regretted that this fundamental work has so long remained hidden among thousands of no less detailed but far less important technical papers and that so little of the material in it has found its way into text-books and general works on vertebrate palæontology and mammalogy.

LATER WORK ON CARNIVORA

Matthew continued at intervals to contribute to the history of the Canidæ and Mustelidæ. Recently (1929) his views on the phylogeny of the Canidæ and on the origin of the bears from a branch of the Canidæ were set forth in an important article in the *Journal of Mammalogy*.¹

Of his subsequent contributions to the Insectivora the most important was his paper of 1913 on "A Zalambdodont Insectivore from the Basal Eocene."² Here he was able to show, first, that the zalambdodont insectivores, like so many groups, conformed to the rule of Holarctic origin and of dispersal into more southern latitudes, the most primitive known forms being found in the Basal Eocene, Eocene and Oligocene of North America, their present-day relatives being found in Madagascar, South Africa and West Africa. The important skull which was the subject of the 1915 paper also enabled him to adduce strong evidence that the peculiar zalambdodont type of upper molar had been derived from a more normal tritubercular type by the inward displacement of the conjoined para- and metacones and by the progressive reduction of the internal cusp.

LATER WORK ON INSECTIVORA

Other important papers dealing with the Insectivora are to be found in "A Revision of the Lower Eocene Wasatch and Wind River Faunas" (with Walter Granger) (1915, 1918),³ and various shorter papers on new

¹1929. The Phylogeny of Dogs. *Journ. Mammalogy*, XI, No. 2, pp. 117-138, 3 figs.

²1913. *Bull. Amer. Mus. Nat. Hist.*, XXXII, Art. XVII, pp. 307-314, Pls. LX, LXI.

³1918. Part V (By W. D. Matthew): *Insectivora* (continued), Glires, Edentata. *Bull. Amer. Mus. Nat. Hist.*, XXXVIII, Art. XVI, pp. 565-657.

fossil zalambdodonts (1903, 1910), leptictids and erinaceids (1903, 1928, 1929), plesiadapids (*Nothodectes*, 1917, *Stehlinius*, 1921). These groups were also dealt with in "Climate and Evolution" (pp. 224-227).

To Matthew the order Insectivora was a "generalized and broadly inclusive order" (in contrast with a more compact specialized order such as the Primates) (1918, p. 568), containing various groups that were unknown descendants of primitive Mesozoic placental insectivores, but which apart from this were not closely related to each other. To this broad assemblage he referred not only the true insectivores, including the zalambdodonts, the leptictids and erinaceids, the talpids, soricids and nesophontids, but also such very diverse forms as (a) the Eocene *Pantolestes* and *Palæosinopa*, having creodont-like teeth but more insectivore-like astragalus; (b) *Apheliscus*, with more tubercular molar teeth and long slender jaw—one of the most puzzling of all these "insectivores"; (c) *Plagiomene* (1918, p. 600), with dilambdodont teeth suggesting those of *Galeopithecus*; (d) *Nyctitherium* (1918, p. 603), with teeth and limb bones suggestive of Chiroptera but provisionally left in the Soricoidea; (e) the Mixodectidæ (1915, pp. 465-467) regarded as possibly allied with the Eocene Tarsiidæ but provisionally left in the Insectivora; (f) the Plesiadapidæ (including *Nothodectes* [= *Plesiadapis*]), the "Apatemyidæ," etc.), regarded (1928, p. 957) as "semi-Primates"¹ (Menotyphla), with enlarged, somewhat rodent-like incisors; (g) the Basal Eocene *Onychodectes* and *Conoryctes*, "transitional in some ways to Tæniodonta." The Lower Eocene *Creotarsus* (1918, p. 611) was placed after the Insectivora under "Order and Affinities Uncertain," since, although its lower teeth showed some resemblances to those of primitive artiodactyls and others to insectivores, its astragalus approximated certain of the creodont types.

Many of these forms differ so widely from the typical insectivores in the dentition that most authorities would have referred the different families to different orders. But Matthew considered the evidence insufficient for placing them in any other given order, and as noted above he held the "Insectivora" as a convenient broad central group. In these doubtful cases he gave less weight to resemblances and differences in the dentition than to the characters of the astragalus, which he regarded as a more constant and sure indicator of ordinal affinities. In his 1928 paper on "The Evolution of the Mammals in the Eocene," he placed (p. 975) the *Plesiadapis* group under the "Order Menotyphla,"

¹1928. The Evolution of the Mammals in the Eocene, Proc. Zool. Soc. London, Pt. 4, 1927. [Published Jan. 12, 1928.] Pp. 947-985, 16 text-figs.

as "semi-Primates" (p. 957) intermediate in some respects between Insectivora (in the restricted sense) and Primates. His final review of these difficult but important problems connected with the Eocene insectivorous groups, which will appear in his forthcoming memoir on the Paleocene mammals (Mem. Amer. Mus. Nat. Hist., 1931), will be awaited with a melancholy interest.

† DIDELPHIS, A CRETACEOUS MARSUPIAL

Another group of primitive mammals to which Matthew made an outstanding contribution was that of the polyprotodont marsupials. In his paper on "A Marsupial from the Belly River Cretaceous. With Critical Observations upon the Affinities of the Cretaceous Mammals" (1916)¹, he described the lower jaw and parts of a skull of a small mammal which had been found by Barnum Brown on Red Deer River, Alberta, embedded beneath a ceratopsian dinosaur skull in a formation of unquestionably Upper Cretaceous age. This jaw and parts of the skull resembled those of a modern opossum in so many points that its relationships with the American polyprotodont marsupials (Didelphiidæ) could not be doubted. This fortunate discovery enabled Matthew to clear up the relationship of Cope's *Thlæodon*, which was now shown to be a polyprotodont marsupial with thickened tubercular cusps on its upper cheek teeth. The presence of ancestral opossums in the Cretaceous went far to confirm the views of Huxley, Dollo and Bensley that this family was practically ancestral to the more specialized marsupials of Australia and South America; and at the same time it gave additional evidence in favor of Matthew's view of the early Holarctic origin of many groups now confined to tropical or southern latitudes.

FOSSIL RODENTS

The fossil rodents of North America also claimed their share of Dr. Matthew's attention. He dealt with them incidentally in various faunal papers, but his most important work on this subject was that "On the Osteology and Relationships of *Paramys* and the Affinities of the Ischyromyidæ" (1910).² Here practically complete skeletons of the Eocene rodent *Paramys* were described and beautifully figured, together with skulls, dentitions, etc., of other Eocene and Oligocene rodents. So far as their dentition and the majority of their skeletal characters were concerned, *Paramys* showed strong evidence of relationships with modern

¹1916. Bull. Amer. Mus. Nat. Hist., XXXV, Art. XXV, pp. 477-500, Pls. II-IV, 4 figs.

²1910. Bull. Amer. Mus. Nat. Hist., XXVIII, Art. VI, pp. 43-71.

rodents, especially the sciuiromorphs, while the other genera were evidently more or less closely related to it. But in all these Eocene forms the insertion of the anterior superficial branch of the masseter muscle was evidently beneath the anterior rim of the malar instead of in front of the orbit, as in modern sciuiromorphs. To Matthew this meant simply that *Paramys* and its allies had retained the more primitive conditions which had been lost by the later sciuiromorphs, but Messrs. Miller and Gidley broke up the Ischyromyidæ into several families and referred them to different superfamily divisions of the rodent order.

FOSSIL PRIMATES

The Lower and Middle Eocene Primates of North America were revised by Matthew in 1915;¹ he was able to revise, confirm and considerably extend the previous reviews by Osborn (1902) and by Wortman (1904), and to add several new species of notharetids and "anaptomorphids." He was also able to trace, more closely than had hitherto been done, the transformation of the very simple triangular and tritubercular upper molar of the older species of *Pelycodus*, through a series of successive horizons, into the quadrate and quadritubercular molar of *Notharctus*. The discovery of good skeletal material of *Notharctus* enabled him to refer it definitely to the suborder Lemuroidea, in spite of the fact that *Notharctus* itself never assumed the specialized dentition of the modern *Lemur*.

Among the Eocene Tarsiidæ, he gave an excellent key for the distinction of the various genera and species and a carefully corrected reconstruction of the famous skull called by Cope "*Anaptomorphus homunculus*," but showed that the name *Anaptomorphus* belonged properly to another genus based on a lower jaw with two lower incisors instead of one; he therefore referred *Anaptomorphus homunculus* to a new genus, *Tetoniuss*, related to *Absarokiuss* and more distantly to *Uintaniuss*, *Shoshoniuss*, etc.

While he had less occasion for intensive study of the higher Primates, including man, Dr. Matthew took a keen interest in their evolution, of which he gave an admirable critical summary in his "Outline and General Principles of the History of Life" (1928, pp. 211-236).²

¹1915. A Revision of the Lower Eocene Wasatch and Wind River Faunas (with Walter Granger). Part IV (by W. D. Matthew): Entelonychia, Primates, Insectivora (part). Bull. Amer. Mus. Nat. Hist., XXXIV, Art. XIV, pp. 429-483.

²1928. Synopsis of Lectures in Paleontology I. Univ. of Calif. Syllabus Series, Syllabus No. 213, pp. 1-253.

EDENTATES

The Edentates naturally received considerable attention from Dr. Matthew, who had occasion to study especially the ground sloths of the Cope Pampæan collection, the edentates collected by Barnum Brown in Patagonia, and the Tæniodonts and Palæanodonts of the Basal and Lower Eocene. "The Ancestry of the Edentates"¹ was treated in an illuminating way in a brief, semi-popular article in 1912, in which the mounted skeleton of *Hapalops*, an ancestor of the ground sloths from the Patagonian Miocene, was fully described. The Palæanodonta were named by Matthew (in 1918)² as a suborder of Edentata, to include the Metacheiromyidæ of Wortman, which were at first referred by the latter to the cheiromyoid division of the Primates. *Metacheiromys* had been redescribed from better material by Osborn, who had referred to it as "An Armadillo from the Middle Eocene (Bridger) of North America." Matthew's *Palæanodon ignavus* was based on a skull, vertebræ, foot-bones, etc., from the Lower Eocene (Wasatch) of Wyoming. This skeleton was shown to be closely related to the Bridger *Metacheiromys* but more primitive in several respects. A careful consideration of the characters and affinities of *Palæanodon* and *Metacheiromys*, in comparison with armadillos and other Xenarthra, with *Manis* and *Orycteropus* and their supposed relatives in the Tertiary of Europe, led Matthew to the conclusion (p. 652) that *Palæanodon* is related to the armadillos, although it retains numerous primitive characters that have been lost in varying degree by the late Tertiary and modern genera and has not developed certain obviously specialized characteristics of all the South American edentates (Xenarthra). Nevertheless, for geographic and faunal reasons (p. 653), he did not think that *Palæanodon* itself was directly ancestral to the Xenarthra but rather that the Xenarthra and *Palæanodon* had been derived from some late Cretacic fauna unknown to us but presumably inhabiting some part of North America which had also contained the immediate ancestors of our Paleocene and Lower Eocene Condylarthra, Taligrada, marsupials, edentates, etc. Comparison with *Manis* and with the supposed edentate remains of the Oligocene and Miocene of France and Germany led him to conclude (p. 654) that: "On the whole, I can find no very conclusive evidence against deriving *Manis* as well as the Loricata (and through them the remaining Xenarthra) from the primitive type represented by *Palæanodon*. Just

¹1912. Amer. Mus. Journ., XII, No. 8, pp. 300-303.

²1918. A Revision of the Lower Eocene Wasatch and Wind River Faunas (with Walter Granger). Part V (by W. D. Matthew): Insectivora (continued), Glires, Edentata. Bull. Amer. Mus. Nat. Hist., XXXVIII, Art. XVI, pp. 565-657.

how direct the ancestors may be in each case is a highly speculative matter. But I think that we are well warranted in concluding that there is, after all, a real affinity between the Pholidota and Xenarthra. They may not necessarily be included in a single order but they do clearly belong in the same natural superorder Edentata.

"*Orycteropus*, however, does not belong in this natural group. So far as I am able to judge, it has no particular relations to the edentate-insectivore group, but is descended rather from the creodont-condylarth group of the primitive placentals. I can find nothing in the skull or skeleton that seems to be characteristically edentate, as distinguished from merely primitive. . . . Elliot Smith believes that the brain indicates affinities rather with the primitive ungulates than with unguiculates; and there is some support for this view in the skeleton, at least so far as condylarthran affinities are suggested. The astragalus has some resemblance to that of typotheres and some other notoungulates, which would be in accord with this derivation."

FOSSIL AND RECENT UNGULATES

Dr. Matthew's contributions to knowledge of the fossil ungulates were numerous and fundamental. His early studies (1897, pp. 299-311, 320, 321) on the skeleton of *Euprotogonia*, from the Torrejon, abound in observations of great interest and value. He remarked that "in every detail of its skeletal structure this relatively primitive condylarth shows a most striking resemblance to the Creodonts. The customary bend of the knee and elbow, the long heavy tail, the semiplantigrade five-toed foot are general points of likeness, and when we compare the separate limb-bones, the close relationship becomes apparent, especially close to the primitive types. . . . In every point where *Euprotogonia* differs from *Phenacodus*, it approaches the Creodonts—or rather approaches that hypothetical form from which descended both Creodonts and Condylarths. It stands therefore in a strictly intermediate position." While Cope had supposed that the Lower Eocene *Phenacodus* was the "five-toed ancestor of the horse," Matthew concluded (p. 309) that "*Euprotogonia* stands nearer to the early Horses than does *Phenacodus*, but I do not think that it can be considered the direct ancestor of *Hyracotherium*. . . . the skeleton exhibits no indications of an advance from the primitive type toward *Hyracotherium* in particular while it has many points of resemblance to *Phenacodus*. We must go somewhat lower down than the Torrejon to find the junction of the Equine and Phenacodont phylæ. . . . it must be supposed that their common ancestor was a clawed

animal, for *Euprotogonia* is in the first stage of development as a hoofed mammal, and shows very little else of the ungulate type of skeleton. In the Torrejon representatives of the horse family, one would expect to find the molars showing some trace of approaching lophodonty, the last one of full size and the astragalus with some indications of a perissodactyl development. In most other respects it might well approximate *Euprotogonia*." While this prophecy even yet remains unfulfilled, the reviewer has entire faith in its truth.

It has been noted above (p. 2) that in the same memorable paper Matthew discredited Professor Cope's theory that the "serial" carpus of *Phenacodus* was primitive, by showing (a) that in *Euprotogonia*, the direct ancestor of *Phenacodus*, the carpus was not "serial" but "alternating"; (b) that it was alternating in the primitive creodonts and peritrichids; (c) that an alternating type could be converted either into a serial type by absorption of the centrale carpi or into a displaced type by fusion of the centrale with the scaphoid.

In his "Memoir on the Bridger Carnivora and Insectivora" (1909), already noted, Matthew gave a very full description of the skull and dentition of *Hyopsodus*. Earlier authors had classed these small animals with the Primates because of the general resemblance of their molar teeth to those of *Notharctus*. Wortman had removed them from the Primates to the Insectivora. Matthew in 1909 allowed the family to remain in that order, although expressing the opinion (p. 512) that "its affinities are in reality closer to the Condylarthra than to the more typical Insectivora." In 1915 (p. 312)¹ he states that "additional skeletal material of *Hyopsodus*, including a well preserved hind foot, served to confirm the above somewhat tentative conclusion and made it advisable to remove the family to the Condylarthra. Its position in the Insectivora has always been anomalous and could only be defended by regarding this order as a sort of catch-basket for primitive unspecialized placentals that could not be placed elsewhere. . . The astragalus, while very primitive, is distinctly of the type peculiar to primitive Carnivora and Condylarthra, as opposed to the characteristic form of the Insectivora or that of the primitive Primates. The teeth exclude it from the Creodonta. In teeth, skull and skeleton characters it compares best with the most primitive among the Condylarthra, and the ungual phalanges, while they are claws rather than hoofs, are but little different from those of

¹1915. A Revision of the Lower Eocene Wasatch and Wind River Faunas (with Walter Granger). Part II (by W. D. Matthew): Order Condylarthra, Family Hyopsodontidae. Bull. Amer. Mus. Nat. Hist., XXXIV, Art. IX, pp. 311-328.

Tetraclænodon. . . .” He then gave a much fuller and more satisfactory definition of the order Condylarthra and of the five families which he finally included in it, namely, Mioclænidæ, Hyopsodontidæ, Phenacodontidæ, Meniscotheriidæ, Pleuraspidotheriidæ.

In his “Revision of the Puerco Fauna” (1897) Matthew had remarked that Cope’s order Condylarthra, as including the three families Phenacodontidæ, Periptychidæ and Meniscotheriidæ, together with the Mioclænidæ (which had been referred to the order by Osborn and Earle), “does not form a genetic line as do the divisions of the more advanced forms but represents the first stage of ungulate evolution. . . . The Condylarthra . . . do not form a homogeneous suborder. Its members had diverged more than they had progressed.” Osborn had removed *Pantolambda* and the Periptychidæ to the Amblypoda. But Matthew, troubled by the intermediate characters of the *Anisonchus* group between *Periptychus* and *Euprotogonia*, left them all in the Condylarthra, where Cope had placed them, although admitting that *Pantolambda* showed an evident relationship to *Coryphodon* of the Wasatch in the teeth, and to a less extent in skeletal structure. Later he referred the Periptychidæ and *Pantolambdæ* to the “order Taligrada”; in 1927 (1928, p. 948) his diagram shows the Taligrada connected with the Amblypoda, although nominally a distinct order. In this recent paper (p. 968) he showed that so far as regards the patterns of the upper molar teeth, the Amblypoda included two very distinct divisions: the first comprising the Paleocene *Pantolambda*, the Lower Eocene *Coryphodon* and the Upper Eocene Mongolian *Eudinoceras*, the second including the Paleocene *Prodinoceras*, the Lower Eocene *Bathyopsis*, the Middle Eocene *Uintatherium* and the Upper Eocene *Eobasileus*. The discovery of *Prodinoceras* showed that the attempts to derive the *Uintatherium* type of molars from those of *Coryphodon* had been in vain and that the two divisions of the Amblypoda were already widely different from each other in the Paleocene.

Matthew’s contributions to the phylogeny of the Artiodactyla were many and varied, too much so, in fact, to be noticed in detail in this all too brief outline of his principal results. He dealt in numerous papers with the camels, oreodonts, hypertragulids, cervids, giraffes, antilocaprids, antelopes, cattle, etc., of the ruminant series, as well as with the anthracotheres and dicotylids of the suillines. In his final diagram of the “phylogeny of the Artiodactyla,” his summary of the actual palæontological succession and of the relationships of the modern families to their Eocene and Paleocene forerunners are clearly set forth. In one of his latest papers, published June 30, 1929, he gives an admirably clear

and practicable "Reclassification of the Artiodactyl Families"¹ into five major groups, as follows: Palæodonta, or primitive Bunodonts, including the American Eocene dichobunids and the Upper Eocene to Miocene Entelodonts; Hyodonts, or pig-like bunodonts, including the pigs, peccaries and hippopotami; Ancodonts, or primitive tetradactyl Selenodonts, a large group including the old bunoselenodonts, the Cænotheriidae and Oreodontidae, with the four-toed short feet of the pig group but with partly or wholly selenodont molars; Tylopoda, or Camel group, including the Xiphodonts and camels; Pecora, or true Ruminant group, including the tragulids, cervids, giraffids, antilocaprids and bovids.

As a result of systematic collecting continued year after year, the American Museum of Natural History amassed an enormous collection of fossil Equidae throughout the long series of Tertiary and Quaternary horizons. Dr. Matthew intensively studied thousands of teeth and skeletal parts of fossil Equidae, not only while identifying and cataloguing the collections but especially in preparing his various faunal papers, including the "Third Contribution to the Snake Creek Fauna" (1924).² With reference to the collection of fossil Equidae from the Snake Creek quarries in Western Nebraska, he wrote (*op. cit.*, p. 154): "This represents many thousands of individuals, no two of them exactly alike in the complex details of tooth construction. If the standards of species distinction that have been accepted by most American students of fossil Equidae were applied conscientiously to this great collection, the result would be to place upon record scores if not hundreds of 'new species' from this one locality. But the thousands of isolated teeth or other fragmentary specimens would clearly show that there are no really constant and uniformly associated distinctions between such 'species.' They are mainly individual differences. . . ." Again, in discussing the relationship of *Pliohippus* to *Equus* and *Hippidium*, he writes as follows:

"I believe, however, that the hard and fast lines of distinction that it is customary among palæontologists (and zoologists) to draw between 'species' are not justified by the evidence; that when one deals with very extensive series of specimens from many closely succeeding stages and many localities, the amount and character of intergrading and mixture of their species characteristics is only explicable as the result of continual admixture of numerous interbreeding strains, so that the 'species' is merely a more or less arbitrary selection of material representing approxi-

¹1929. Bull. Geol. Soc. Amer., 40, pp. 403-408.

²1924. Bull. Amer. Mus. Nat. Hist., L, Art. XI, pp. 59-210.

mations to a strain locally and temporarily dominant. It is to be pointed out in this connection that interbreeding does not produce exact intergradation in the characters of a series of specimens but various admixtures of more or less distinct and definite characters. . . . From this viewpoint the more detailed affinities of the later Equidæ are matters of degree of relationship or dominance of one or another ancestral stock in a complexity of intercrossing strains which only slowly and gradually take on that complete infertility between progressively diverging groups which brings about definite and permanent distinctness." In his application of this theory to the origin of the modern *Equus*, he suggested (p. 168) that "*Equus* shows an admixture, somewhat varying in its different species, of progressive characters, some of which are assumed earlier by typical *Plihippi*, some by typical *Hipparions*; there is nothing in the generic characters of either genus to exclude it from the ancestry of *Equus* but all the better-known species of each are off the direct line, although some are perhaps not excluded from participation in some degree in the ancestry of the modern horses."

In view of all this it was a matter of considerable interest that soon afterward (1924) Dr. Matthew and his assistant George Gaylord Simpson found in the Blanco (Middle Pliocene) formation of Texas two skeletons of a fossil equine which proved to be intermediate in character between *Plihippus* and *Equus*. This stage of evolution was accordingly named by Matthew, *Plesippus* (near horse.)¹

As a result of his great mass of detailed knowledge of the fossil Equidæ, Dr. Matthew was able to prepare an excellent handbook on the Evolution of the Horse and an authoritative and critical review of the same subject, published in the *Quarterly Review of Biology*, 1926, with many beautiful illustrations and diagrams. The same article also contains his diagram showing the divergent evolution of the perissodactyls in the older Tertiary, which summed up the results, primarily of his own studies but with due regard to the views of other authorities, on the phylogeny of the numerous families and subfamilies of rhinoceroses, lophiodonts, tapirs, horses and other perissodactyls.

VARIOUS FAUNAL PAPERS

Concerning Matthew's later papers on fossil mammalian faunæ, especially those of the Miocene and Pliocene of the western states, India and Mongolia, one can only say in a word that they record thousands of

¹1924. A New Link in the Ancestry of the Horse. Amer. Mus. Novitates, No. 131, Sept. 23, 1924, pp. 1, 2.

facts that are important to specialists and that they abound in discussions and views of wider interest. For example, in his review of the Siwaliks fauna¹ as a result of his studies in the Indian and British Museums, he made scores of important observations on the phylogeny of the bears, giraffes, camels and other groups and gave new evidence as to the correlation of the Siwalik horizons with those of the late Tertiary and Pleistocene of Europe and North America.

Similarly in his various brief articles on the fossil mammals of Mongolia and China, as a result of his own and of his colleagues' field observations and Museum studies, he was able to determine not only the relationships of the mammals but also the approximate positions of the faunæ, in comparison with the better known faunæ of Europe, India, North and South America.

In connection with South American palæontology he described (1915, pp. 429-433)² a curious little lower jaw from the Lower Eocene Wasatch of Wyoming, which he referred to the notoungulate order of Entelonychia. He pointed out that the molar teeth of this form resembled those of the Patagonian *Notostylops* and related types in general pattern and in the possession of certain features peculiar to the notoungulates. He thought it improbable that these resemblances could be due to convergence and therefore regarded the new form *Arctostylops* as probably an aberrant offshoot from the northern ancestors of the extinct South American ungulates. It was therefore a matter of great interest that one of the Museum expeditions in Mongolia discovered there in a formation of possibly Paleocene age a diminutive lower jaw, together with the upper teeth of a mammal of the notoungulate type, that closely resembled *Arctostylops*.³ Here, then, was direct evidence for the view so long advocated by Matthew upon other grounds, namely, that the peculiar extinct South American orders had sprung from some very early immigrant from northern North America, which in turn had been derived from north Asiatic ancestors.

GENERAL THEORIES

In conclusion, we come to the more general theories of mammalian origin and dispersal for which Dr. Matthew was far more widely known than for his detailed technical monographs, although the latter must

¹1929. Critical Observations upon Siwalik Mammals (Exclusive of Proboscidea). Bull. Amer. Mus. Nat. Hist., LVI, Art. VII, pp. 437-560.

²1915. A Revision of the Lower Eocene Wasatch and Wind River Faunas (with Walter Granger). Part IV (by W. D. Matthew): Entelonychia, Primates, Insectivora (part). Bull. Amer. Mus. Nat. Hist., XXXIV, Art. XIV, pp. 429-483.

³1929. Additions to the Fauna of the Gashato Formation of Mongolia. (With Walter Granger and George Gaylord Simpson). Amer. Mus. Novitates, No. 376, Oct. 7, 1929, pp. 1-12.

always be regarded by active students of fossil mammals as of far greater importance and value. The first was his theory of the arboreal origin of the Mammalia, which was set forth in a brief article in the *American Naturalist* in 1904.¹ Here he noted that, while Huxley, Dollo and Bensley had adduced strong evidence for the arboreal origin of the marsupials, he had for some time been of the opinion that this was true not only of the marsupials but of the placentals as well. In support of this view he cited various skeletal characters of the oldest creodonts, protungulates, rodents, primates, etc., which appeared consistent with the hypothesis that they were either semiarboreal to arboreal or had been derived from arboreal Mesozoic mammals. He then reviewed the vertebrate faunæ and life zones of the later Mesozoic era, suggesting that while the giant reptiles for the most part held the terrestrial field, the mammals had remained as small forest-living, arboreal or semiarboreal forms, but that with the great climatic changes at the close of the Mesozoic and the consequent spread of upland conditions, the mammals had abandoned their arboreal habitat and exploited the areas left more or less vacant by the giant reptiles. Against this theory Dr. Gidley² later brought the objection that certain of the characters cited for arboreal ancestry by Matthew (such as the five-toed spreading hands and feet, long tail) might be merely primitive characters inherited from reptilian ancestors. But to the reviewer it seems that the resemblances of the Paleocene mammals to the reptiles are only very distant and general ones, while their resemblances to the arboreal opossum are much more specific, though their former arboreal adaptations even in the Paleocene, had already undergone considerable reduction in response to the various terrestrial adaptations which they were then assuming.

By far the most famous of Dr. Matthew's works was his "Climate and Evolution" (1915).³ His main theses were: (a) the relative permanency of the great ocean basins, as a result of isostatic relations of water and land masses; (b) the origin of most of the orders and families of mammals in Holarctic areas and the subsequent spreading of many of them into southern latitudes; (c) the deployment in the southern countries of the descendants of immigrants from the north, into new faunæ like those of the marsupials of Australia or the extinct notungulates of South America; (d) the importance of geographic isolation in protecting the descendants of archaic stocks from the destructive com-

¹1904. The Arboreal Ancestry of the Mammalia. *Amer. Naturalist*, XXXVIII, pp. 811-818.

²1923. Paleocene Primates of the Fort Union, with Discussion of Relationships of Eocene Primates. *Proc. U. S. Nat. Mus.*, LXIII, Art 1, pp. 10-38, Pls. I-v.

³1915. *Ann. N. Y. Acad. Sci.*, XXIV, pp. 171-318, 33 text figs.

petition of the higher placental orders; (e) the impelling force of secular climatic changes, such as the great lowering of temperatures at the various periods from the Permian onward, in causing increased severity of Natural Selection for higher body temperature, for larger and better brains and other superior adaptations against extremes of heat and cold.

In connection with this general theory, Dr. Matthew vigorously opposed the hypothetical building of great "land bridges" across wide ocean spaces to account for similarities between animals and plants on opposite shores of the oceans. He was able to adduce evidence, for example, that such forms as the extinct chrysochlorid-like *Necrolestes* of Patagonia and the true chrysochlorids of South Africa owed their resemblances not to direct relationship but to a common origin from northern stock of Paleocene or Eocene age. The peopling of oceanic islands with small mammals he attributed to chance transportation, as by natural rafts, hurricanes, etc., rather than to former connections with the mainland. In this connection one naturally recalls his carefully considered palæogeographic maps ("Hypothetical Outlines of the Continents in Tertiary Times," 1906)¹ and polar projections, which greatly assist in the visualization of his views on the migrations of mammals.

The numerous criticisms and objections which were called forth by this theory naturally cannot be considered in the present paper; but it may be permissible to express the feeling that, although Doctor Matthew's general theory of mammalian dispersal may eventually be modified in detail, involving possibly the existence of certain land bridges whose reality he denied, there will be a large residue of well tested evidence in favor of the Holarctic origin and subsequent dispersal of many families of placental mammals along the general lines indicated in his maps.

SUMMARY

In brief summary the papers cited here represent Doctor Matthew's chief contributions to knowledge of fossil and recent carnivores, insectivores, primates, rodents, edentates, marsupials, condylarths, peripitychids, amblypods, artiodactyls, etc. In addition but only glanced at in this scant review, are his faunal lists of Tertiary mammal horizons, his studies in many fields and museums of the Tertiary and Quaternary faunæ of North and South America, Europe, India, Mongolia, Burma, Java, etc., and his analyses of these faunæ and of their migrations in past ages. Some of his more general conclusions may also be reiterated: on

¹1906. Bull. Amer. Mus. Nat. Hist., XXII, pp. 353-384, 7 text figs.

the mode of deposition of the mammal-bearing horizons of the west, on the origin of the "serial" carpus, on the merits of the so-called "horizontal" as compared with the "phylogenetic" classifications, etc., and especially his well known views on the arboreal origin of the mammals, on the relative permanency of ocean basins, on the doctrine of isostasy in its bearing on the problems of geographic distribution, on the Holarctic origin of the majority of the mammalian faunæ of the world. All this, he inferred, was under the control of the secular lowering of temperatures that repeatedly caused the onset of harsh and variable climates, thus intensifying the pressure of Natural Selection toward higher body temperatures and superior protection against the extremes of heat and cold.

Thus, due to the lasting importance of his contributions to vertebrate palæontology, and to the stimulating nature of his publications, it cannot be doubted that in time to come Dr. Matthew's colleagues, his students and successors will push on toward the solutions of the major problems of earth-history and evolution, which were always his ultimate objectives; nor will these workers fail to add greatly to the new facts of science, which he prized far more highly than its theories.

